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Abundance, biomass and diversity of soil macrofauna in savanna woodland and associated managed habitats

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With 4 figures

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1. Introduction

Rates of organic matter decomposition in soils are known to be affected by the activities of soil macrofauna (PETERSEN & LUXTON, 1982) and must be taken into account in studies of litter decay and nutrient cycling (SWIFT, 1987). Experiments on leaf litter decomposition that exclude macrofauna show a slower rate of breakdown (CROSSLEY & WITKAMP, 1966; EDWARDS *et al.*, 1970) and retarded nutrient release (WITKAMP & AUSMUS, 1976) probably due to reduced microbial activity.

Detritus feeders may process up to 30% of the annual dead organic matter input to most soils (KITAZAWA, 1967) and affect decomposition of such material through fragmentation, inoculation with microbial spores and/or physical disturbance. Fragmentation can enhance leaching of soluble materials by rainwater, increase the available surface area of organic matter for micro-organisms and in some instances increase mineralisation rates on conversion of plant litter to faeces (POMIANOWSKA-PILIPIUK, 1976). Faecal material may also contain inocula of micro-organisms as has been shown for millipedes (ANDERSON & BIGNELL, 1980; HANLON, 1981), isopods (REYES & TIEDJE, 1976; HASSALL & RUSHTON, 1984) and earthworms (SATCHELL, 1967) or have increased levels of soluble carbohydrate that microbial activity (LAVELLE *et al.*, 1980).

The majority of soil animal studies refer to species living in temperate habitats. Despite their importance in influencing nutrient release the effects of soil fauna on decomposition in tropical ecosystems is poorly understood, with the possible exception of termites (LEE & WOOD, 1971) and earthworms (LAVELLE, 1983, 1988). This is especially true for tropical savannas and the agricultural systems derived from them.

An understanding of the composition, relative abundance and biomass of soil fauna identifies the key taxonomic groups and is a first step in the understanding of their role in nutrient dynamics. This is particularly important in savannas due to the wide variety of habitat types, both natural and managed, that exist on soils of poor nutrient status. The current paper takes a divisive approach (USHER *et al.*, 1979) and describes a survey of soil macrofauna in a natural savanna woodland and four managed systems on granite sand soils in the highveld of Zimbabwe.

This local study forms part of an international programme on tropical soil biology and fertility (TSBF) which has objectives aimed at the management options for improving tropical soil fertility through biotical processes (SWIFT, 1986). The effects of certain soil macrofauna may have considerable beneficial implications for any management proposals.

2. Methods

2.1. Study site descriptions

Soil macrofauna were sampled from 5 habitat types within the Grasslands Research Station at Marondera, Zimbabwe (18° 10' S, 31° 30' E). The climate is strongly seasonal with 80% of the mean annual rainfall of 846 mm falling between November and March, while the onset of rains and total yearly precipitation are highly variable. The soils are sandy, strongly leached and classified as granite derived alfisols.

The natural habitat chosen was 6.5 ha dominated by the trees *Brachystegia spiciformis* (BENTH.) and *Julbernardia globiflora* (TROUPIN.) termed deciduous miombo savanna woodland (WILD & BARBOSA, 1967) and is referred to here as miombo (MWD). This area had remained free from significant human disturbance for forty years. Consistent with other savanna woodlands the vegetation on this site shows considerable spatial heterogeneity in composition and abundance, a conspicuous feature being open areas with little or no higher plant cover and with the surface soil often capped with blue-green bacteria. This variation was included in the faunal survey by selecting the following sample sites from a classification of the vegetation types following CAMPBELL *et al.* (1988):

- (1.) closed canopy woodland dominated by *B. spiciformis* (CB)
- (2.) closed canopy woodland dominated by *J. globiflora* (CJ)
- (3.) an open area with some *B. spiciformis* regeneration (OB) and
- (4.) an open area with some *J. globiflora* regeneration.

These four vegetation sub-types cover 78% of the woodland with open areas of mixed *B. spiciformis* and *J. globiflora* making up 16% of the remainder.

The clearance of woodland in 1981 less than 500 m from the miombo site and subsequent maize cultivation (M) with a contiguous area of grassland fallow (F) provided two agricultural sampling sites. At the time of sampling the maize crop was well established with individual plants between 2.0 and 2.5 m high. The soil on this site is ploughed in October as preparation for planting and is rotivated in early December to remove weeds. Some inorganic nitrate fertilisers are applied. The area of fallow has followed a succession from early pioneer grasses and is now dominated by perennial grasses with some legumes and tree regeneration but as yet there is no canopy cover.

Samples were also taken from beneath a small stand (less than 1 ha) of mixed indigenous trees adjacent to the maize field. Tree species present on this site include *B. spiciformis*, *J. globiflora*, *Parinari curatellifolia* (PLANCH.), *Strychnos spinosa* (LAM.) and a *Rhus* species. This site is referred to as disturbed miombo (DM) as it was similar to the natural miombo woodland but the proportions of the tree species differed. Leaf fall from these trees produced a thick litter and several species of grass were present in the understorey. A thick litter layer was also present beneath a stand of mature eucalyptus trees (*Eucalyptus grandis*) adjacent to the miombo woodland. Soil macrofauna were also sampled from this area (E).

All sites were sampled during the period from 1st to 5th February 1988 which represents the middle of the only rainy season. In 1988 the first rains of the season began later than expected on 1st December but at the time of sampling total rainfall was above the 30 year average.

2.2. Sampling procedure

In each site a series of 12, 25 cm × 25 cm × 30 cm soil monolith samples were taken following the methods described in the Tropical Soil Biology and Fertility methods handbook (ANDERSON & INGRAM, 1989). In the miombo woodland each sample was located within the habitat sub-types on a random stratified basis. Sampling restrictions in the other habitats prevented total randomisation and so samples were taken in a linear sequence at 5 m intervals from a randomised starting point. The scale of variation in the vegetation on these sites produced randomised sampling with the linear method, especially with respect to the ground flora.

A metal sleeve was placed around each monolith to prevent any lateral movement of animals and removable slats enabled layers within the soil profile to be sorted separately. In each case the mean depth of the litter layer was recorded, then the litter was removed and hand sorted for macrofauna with body length greater than 2 mm. The organic layer and root zone (0–8 cm) was removed and sorted, followed by soil layers 8–18 cm and 18–30 cm. Any animals were recorded and collected.

Field identification to family or genus was not possible for every group, consequently the taxonomic unit for recording was standardised to order. A distinction was made between the larvae and adults of certain orders, particularly the Coleoptera and Diptera because of the functional differences in the life history stages of these animals. All orders were collected except the Hymenoptera which in these samples consisted primarily of several ant species (Formicidae). In many cases ants were too numerous in the sample to collect efficiently and were often less than 2 mm in body length. Presence or absence from each layer was recorded.

The mean abundances of individuals from each order were calculated from the twelve samples and standardised to individuals per m². Conversion of counts to biomass were made by multiplication of the mean body mass of individuals from the particular habitat type by the population density estimates for each sample.

Body mass was measured in the laboratory to 0.001 g on a Mettler PM460 electronic balance. No attempt was made to correct for the mass of gut contents.

3. Results

3.1. Variation within the miombo woodland

A total of 9 orders of macrofauna were represented in monolith samples from the four habitat sub-types within the miombo woodland. Population density estimates for each order are given in table 1. Diplopoda and Coleopteran larvae were most abundant in the closed habitats whilst termites dominated numerically in the open areas. The presence of segmented worms in the closed sites and even in the OJ area was not expected given the sandy texture of the soil and the long periods without rainfall during the winter. However several endemic earthworm species have well developed adaptations to drought stress (REINECKE, 1983).

The established tendency of soil fauna to show aggregated distributions contributed to the high variance in population density estimates, especially for the Isoptera. A log (n + 1) transformation of the data normalised the frequency distributions and subsequent ANOVA showed significant between site differences in abundance within the miombo woodland for earthworms ($F_{3,43} = 4.23$, $P < 0.05$) and beetle larvae ($F_{3,43} = 13.36$, $P < 0.001$). However, there was no significant difference in total abundance of all soil macrofauna between the habitat sub-types ($F_{3,43} = 0.76$, $P < 0.01$).

Estimates of biomass for each order are shown in fig. 1. Diplopods or Coleopteran larvae were dominant in all sites within the miombo due to their relatively large individual masses. This is also true for the Annelida which accounted for 29.2% of the CJ faunal biomass. Isoptera were less important with only 1.0% of total biomass in the CB site; they were not recorded in the CJ samples and in rank order were behind the Diplopoda in the OB (26.9%) and OJ (20.9%) sites.

Significant differences between the habitat sub-types in the total biomass of soil macrofauna ($F_{3,43} = 4.75$, $P < 0.01$) are illustrated in fig. 2(a). The lowest overall biomass occurred in the open habitats. The lack of canopy cover would increase exposure to sunlight and direct rainfall in the open areas which may create unsuitable conditions of microclimate for many groups. The

Table 1. The density of soil fauna (± 1 s.e.) in habitat subtypes within the miombo woodland site, Marondera.

	Density (Individuals \times m ⁻²)			
	Closed <i>Brachystegia</i>	Open <i>Brachystegia</i>	Closed <i>Julbernardia</i>	Open <i>Julbernardia</i>
Annelida	4.0 \pm 2.1	0	14.7 \pm 5.7	2.0 \pm 2.0
Isopoda	6.7 \pm 3.7	0	0	0
Arachnida	10.7 \pm 4.2	2.6 \pm 1.8	16.0 \pm 6.2	2.0 \pm 2.0
Diplopoda	44.0 \pm 14.1	18.7 \pm 6.2	20.0 \pm 9.9	
Thysanura	1.3 \pm 1.3	2.6 \pm 1.8	1.3 \pm 1.3	2.0 \pm 2.0
Orthoptera	8.0 \pm 2.4	0	1.3 \pm 1.3	0
Dermaptera	12.0 \pm 4.0	0	10.7 \pm 4.2	0
Dictyoptera	12.0 \pm 6.9	2.6 \pm 1.8	6.7 \pm 3.0	2.0 \pm 2.0
Isoptera	27.2 \pm 21.0	153.3 \pm 68.8	0	281.6 \pm 208.0
Diptera larvae	9.3 \pm 4.2	1.3 \pm 1.3	4.0 \pm 2.1	0
Coleoptera				
adults	8.0 \pm 5.4	4.0 \pm 2.9	1.3 \pm 1.3	2.0 \pm 2.0
larvae	36.0 \pm 6.6	9.3 \pm 3.7	48.0 \pm 9.6	6.1 \pm 2.9
Total	178.7 \pm 28.7	194.7 \pm 69.2	122.7 \pm 15.0	338.0 \pm 204.2

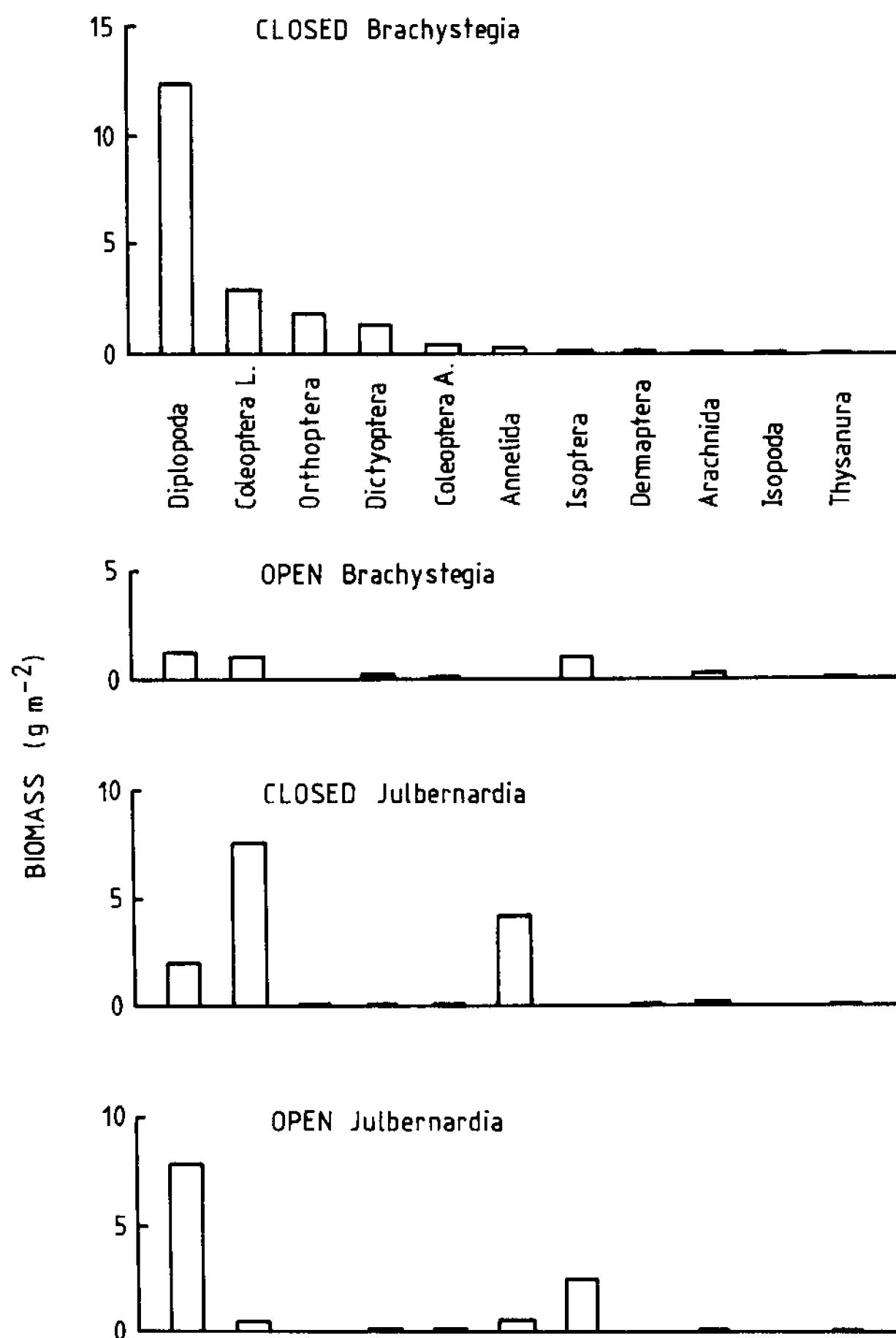


Fig. 1. Estimates of soil macrofauna biomass (g m^{-2}) for each taxonomic order in habitat sub-types within the miombo woodland.

organisms recorded in any significant numbers were those buffered from environmental extremes either by living permanently in the soil (e.g. Coleopteran larvae, certain Isoptera); or that have the ability to burrow into the soil (e.g. Diplopoda). The sandy nature of the open sites within the miombo woodland and the relative absence of dense root systems, particularly from grass species, may make these sites attractive to burrowing organisms and may also explain the prevalence of soil nesting termites in these areas.

Estimates of diversity (mean number of orders per sample) for each of the habitat sub-types are given in fig. 2(b). Despite the simplicity of this diversity index there were significant between site differences with higher diversity within the closed sites ($F_{3,40} = 6.95$, $P < 0.001$). Organisms sensitive to environmental extremes such as the Isopoda, Dermaptera, Orthoptera and Annelida were absent from the open habitats. The increase in habitat complexity and the buffering effects of ground layer vegetation and leaf litter are the most likely explanations for the observed differences.

Several authors have suggested relationships between the quantity and quality of leaf litter and the abundance of soil fauna (see review by PETERSEN & LUXTON, 1982). There were no significant correlations between litter thickness and abundance, biomass or diversity within the miombo habitat sub-types. However pooling the data showed higher diversity (D) with increased litter depth (L) across sites (linear regression; $D = 2.40 + 1.08 L$, $r = 0.494$, $P < 0.001$, $n = 44$). Differences in

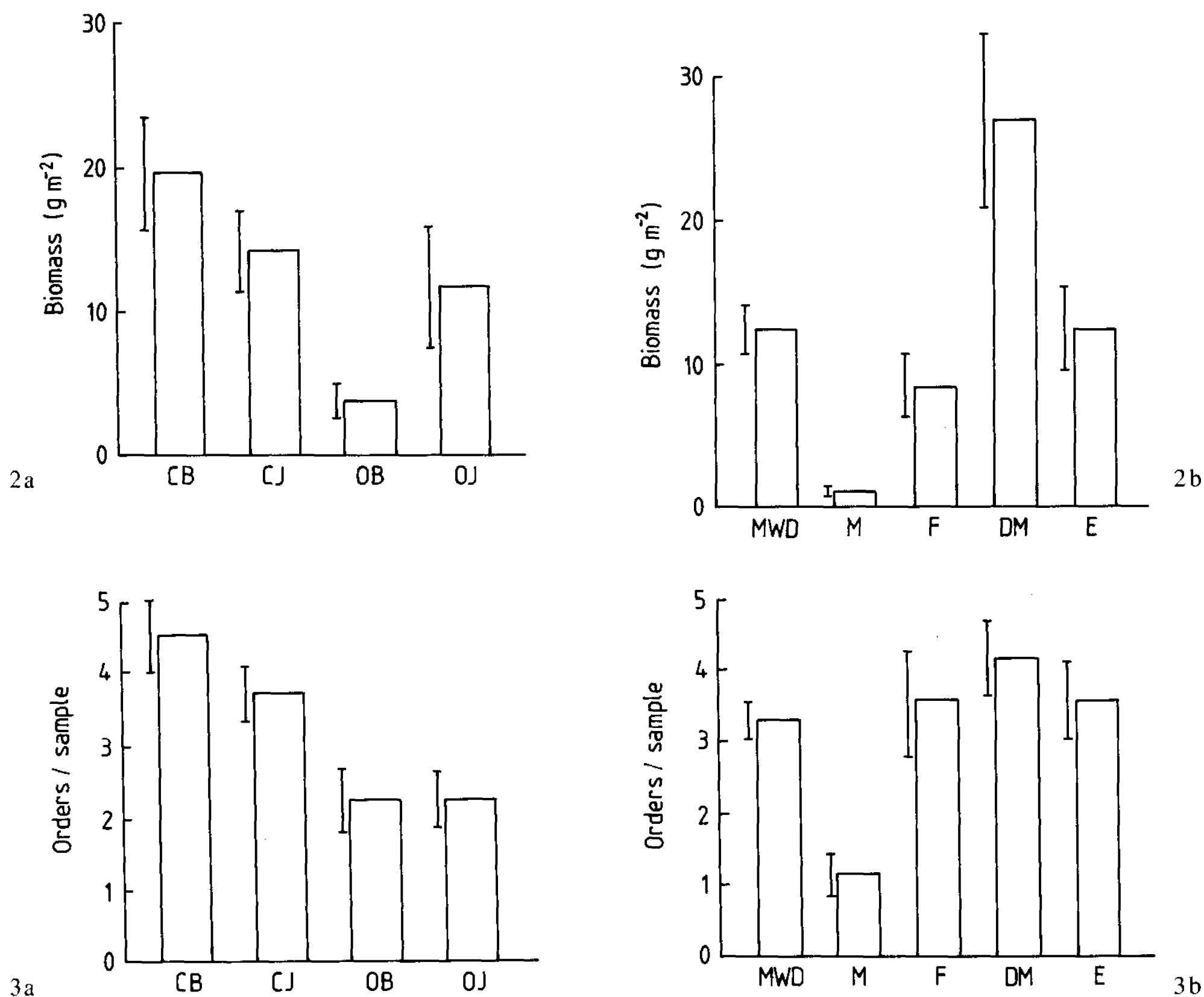


Fig. 2(a). Comparison of total soil macrofauna biomass ($\text{g m}^{-2} \pm 1 \text{ s.e.}$) for each habitat sub-type within the miombo woodland. CB, closed *B. spiciformis*; OB, open *B. spiciformis*; CJ, closed *J. globiflora*; OJ, open *J. globiflora*. Differences between means were significant; ANOVA $F_{3,23} = 4.75$, $P \leq 0.001$. (b). The mean number of orders per sample ($\pm 1 \text{ s.e.}$) for each habitat sub-type ANOVA $F_{3,40} = 6.95$, $P \leq 0.001$.

Fig. 3(a). Comparison of total soil macrofauna biomass ($\text{g m}^{-2} \pm 1 \text{ s.e.}$) between the miombo woodland (MWD), maize field (M), fallow (F), disturbed miombo (DM) and eucalyptus (E) habitats. ANOVA $F_{4,91} = 7.64$, $P \leq 0.01$. (b). The mean number of orders per sample ($\pm 1 \text{ s.e.}$) for each habitat type. ANOVA $F_{4,91} = 4.82$, $P \leq 0.01$.

litter thickness only explain 24.4% of the variance in diversity. There were no significant correlations between litter thickness and abundance or biomass using the combined data.

3.2. Comparison between natural and managed habitats

Abundance estimates varied widely between the habitats both for individual orders and for total macrofauna (table 2). The abundance of the orders sampled from the maize field were low and several groups were not recorded. Highest total densities occurred in the disturbed miombo whilst abundance estimates from samples beneath the eucalyptus trees were comparable with those from the miombo woodland. Again using normalised data [$\log(n + 1)$] there were significant between site differences in overall density ($F_{4,31} = 7.67$, $P < 0.001$).

Biomass estimates for each taxonomic unit across the habitats are compared in table 3. As in the miombo woodland, Diplopods form the dominant group when present, and accounted for 52–77% of total biomass. Although not recorded using soil monoliths diplopods are also known to occur within the maize field but probably as short term migrants from adjacent habitats. Failure to record

Table 2. The abundance of soil fauna (± 1 s.e.) in different habitat types within the Grasslands Research station, Marondera.

Taxonomic Unit	Density (Individuals $\times m^{-2}$)				
	Miombo Woodland	Maize Field	Fallow	Disturbed Miombo	<i>Eucalyptus</i> Stand
Lumbricidae	5.46 \pm 1.9	0	0	4.00 \pm 2.9	6.68 \pm 3.1
Isopoda	6.72 \pm 1.9	0	0	4.70 \pm 6.9	0
Arachnida	8.36 \pm 2.2	6.77 \pm 3.6	8.00 \pm 4.6	29.33 \pm 11.2	22.70 \pm 7.0
Diplopoda	26.24 \pm 5.3	0	0.67 \pm 3.6	89.33 \pm 25.6	0
Thysanura	1.82 \pm 0.8	0	4.00 \pm 2.1	0	0
Orthoptera	2.56 \pm 0.9	1.28 \pm 1.3	4.00 \pm 2.9	0	5.33 \pm 2.4
Dermaptera	6.18 \pm 1.7	0	1.28 \pm 1.3	1.28 \pm 1.3	5.33 \pm 2.3
Dictyoptera	6.18 \pm 2.2	2.83 \pm 2.8	5.30 \pm 3.0	13.33 \pm 5.1	
Isoptera	100.40 \pm 43.5	0	50.70 \pm 22.1	49.33 \pm 18.1	18.70 \pm 14.6
Diptera larvae	4.00 \pm 2.8	2.70 \pm 2.0	8.00 \pm 3.2	1.28 \pm 1.3	2.70 \pm 2.0
Coleoptera					
Adults	4.00 \pm 1.7	5.30 \pm 2.3	9.33 \pm 5.4	15.33 \pm 8.0	8.00 \pm 2.4
Larvae	26.55 \pm 4.2	10.67 \pm 5.3	2.72 \pm 1.8	25.28 \pm 7.0	41.33 \pm 13.4
Others*	0	1.28 \pm 1.3	13.33 \pm 6.8	0	9.33 \pm 3.7
Total	197.00 \pm 42.0	30.70 \pm 8.7	125.30 \pm 27.6	248.00 \pm 41.0	125.00 \pm 35.0

Others (*) includes adult Diptera, Orthoptera (Mantises) and Lepidoptera (caterpillars) Inter-site differences in total density were significant; ANOVA $F_{4,91} = 7.67$, $P < 0.001$ (data normalised by log $n + 1$ transformation).

Table 3. The biomass of soil fauna (± 1 s.e.) in different habitat types within the Grasslands Research Station, Marondera.

Taxonomic Unit	Biomass g $\times m^{-2}$				
	Miombo Woodland	Maize Field	Fallow	Disturbed Miombo	<i>Eucalyptus</i> Stand
Annelida	1.305 \pm 0.52	0	0	0.640 \pm 0.44	0.352 \pm 0.28
Isopoda	0.015 \pm 0.01	0	0	0.128 \pm 0.07	0
Arachnida	0.150 \pm 0.05	0.069 \pm 0.04	0.176 \pm 0.09	0.208 \pm 0.08	0
Diplopoda	5.710 \pm 1.46	0	6.512 \pm 2.20	20.544 \pm 5.89	0
Thysanura	0.028 \pm 0.01	0	0.096 \pm 0.05	0	0
Orthoptera	0.469 \pm 0.18	0.019 \pm 0.02	0.048 \pm 0.04	0	0.347 \pm 0.20
Dermaptera	0.083 \pm 0.02	0	0.003 \pm 0.00	0.001 \pm 0.00	0.368 \pm 0.16
Dictyoptera	0.476 \pm 0.22	0.048 \pm 0.05	0.048 \pm 0.02	0.352 \pm 0.13	0.107 \pm 0.04
Isoptera	0.787 \pm 0.36	0	0.096 \pm 0.04	1.456 \pm 0.46	0.777 \pm 0.63
Diptera larvae	0.048 \pm 0.02	0.027 \pm 0.02	0.272 \pm 0.11	0.001 \pm 0.00	0.109 \pm 0.07
Coleoptera					
adults	0.178 \pm 0.08	0.187 \pm 0.08	0.672 \pm 0.31	0.864 \pm 0.44	0.360 \pm 0.11
larvae	3.246 \pm 0.61	0.715 \pm 0.36	0.256 \pm 0.13	3.088 \pm 0.85	5.911 \pm 0.29
Others*	0	0.080 \pm 0.08	0.272 \pm 0.13	0	0.037 \pm 0.02
Total	12.48 \pm 1.76	1.144 \pm 0.39	8.448 \pm 2.29	27.200 \pm 6.01	10.256 \pm 2.82

Others* includes adult Diptera, Lepidoptera (caterpillars) and Orthoptera (Mantises) Inter-site differences in total biomass were significant; ANOVA $F_{4,91} = 11.31$ $P < 0.001$ (data normalised by log $n + 1$ transformation).

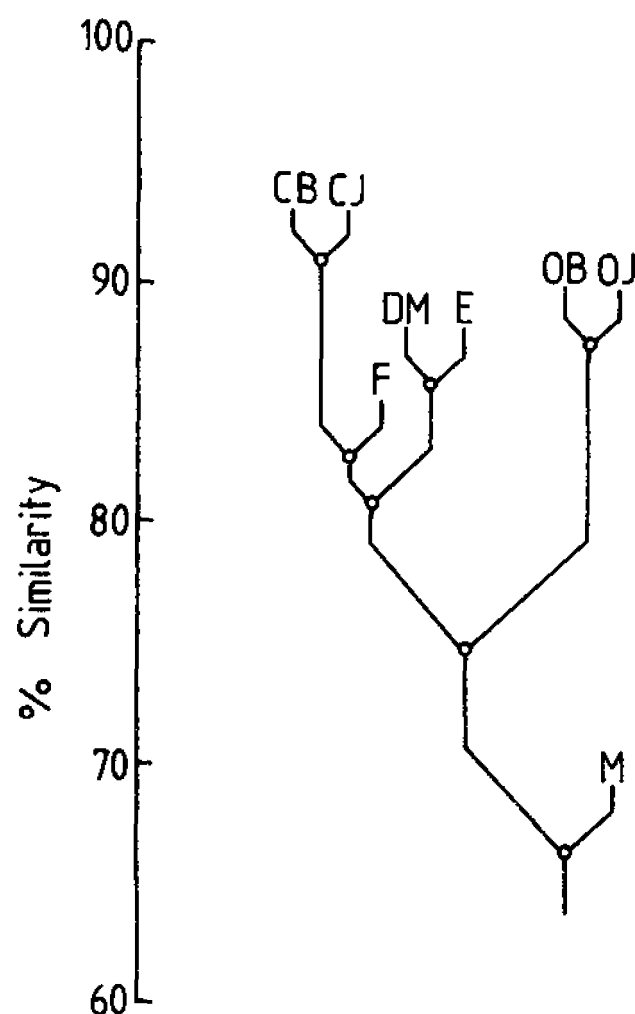


Fig. 4. Classification of habitats based on SØRENSEN's quotient of similarity. Labels as for Fig. 2(a). and 3(a).

Diplopods in the eucalyptus site does not imply their total absence but the environmental quality of the soil, particularly with respect to low pH values, may restrict this group to temporary visits.

Phytophagous groups such as Coleopteran larvae were well represented in all of the habitats and accounted for 57.6% of the biomass in the eucalyptus site and 62.5% in the maize field. Nearly all Coleopteran larvae recorded were Melonithiformes. These are often considered as agricultural pests as they consume the roots of the crops (WALLWORK, 1971). Estimated densities of 10.67 ± 5.3 beetle larvae m^{-2} in the maize may have effects on the root systems of the plants.

The total biomass of soil macrofauna for each site, summarised in fig. 3(a), shows significant differences between the sites ($F_{4,31} = 7.64$, $P < 0.01$). The mixed tree site shows the highest biomass but is dominated by the diplopods, without this group a total biomass value of 10 gm^{-2} would be comparable with the miombo, fallow and eucalyptus sites.

Differences in diversity between the sites were small; only samples from the maize field recorded less than 3 orders per sample [fig. 3(b)]. Nevertheless this was sufficient to significantly increase the between site variance.

As with the miombo habitat sub-types there were no within site relationships between the abundance of soil macrofauna [$\log(n + 1)$] and litter thickness (L). Combining the data from all sites produced a significant positive relationship (linear regression; $\log(n + 1) = 1.78 + 0.183L$, $r = 0.253$, $P < 0.02$, $n = 91$) but litter thickness only explained 6.4% the variance in abundance. No significant correlations were found for the effect of litter thickness on the biomass of soil macrofauna.

Samples taken from areas with a deep litter layer in the eucalyptus site had significantly higher diversity (D) (linear regression; $D = 0.874 + 1.41L$, $r = 0.875$, $P < 0.001$, $n = 12$). Some of the determinants of diversity such as temperature, humidity and food availability are likely to correlate with litter thickness but the relationship is complex, subject to high variance and not necessarily linear.

4. Discussion

Sampling methods used in this study were not necessarily suitable for all the disparate groups of soil macrofauna. Several large millipede species, members of the Ondontopygidae and Spirostreptidae families, were not recorded in the monolith samples but are known to be present in the miombo woodland and as temporary migrants into the maize field (personal observation). A separate survey of the mound building termite *Cubitermes sankurensis* [DANGERFIELD, in press.] estimated their densities in closed *Brachystegia* habitats to be $204 \pm 20 \text{ m}^{-2}$ higher than the estimate from monolith

sampling. Specialist sampling of individual groups is required to quantify the scale of spatial variation and there is also a need to add a temporal component to the present static measures. Despite these limitations differences between habitat types were highly significant. The efficiency of hand sorting in these sandy soils was probably high and comparable to those reported by LEAKEY & PROCTOR (1987).

Density estimates for Dictyoptera, Thysanura and Orthoptera in the present study were similar to those summarised by MALAISSE (1978) for miombo woodland in Zaire. Population densities of Isoptera (1530 m^{-2}) and adult Coleoptera (21.29 m^{-2}) were much higher in Zairian miombo whilst population densities of Dermatera (0.46 m^{-2}) and Diplopoda (4.17 m^{-2}) were an order of magnitude lower.

The spatial patterns of abundance and biomass for many organisms not only vary between habitat types but also within habitats. Intra-site heterogeneity is especially important for certain groups of soil macrofauna which tend to form natural aggregations and is clearly illustrated in the present study both with the Isoptera and Diplopoda, and for the whole soil fauna assemblage within the miombo woodland. Spatial variation with respect to habitat type was most significant for the taxonomic groups containing species that live in the litter layer or at the soil-litter interface. Truly soil dwelling groups, such as Coleopteran larvae, were more evenly distributed which suggests a strong influence of microclimate on patterns of distribution. Such patterns of aggregation in soil fauna populations will increase the degree of spatial heterogeneity in decomposition processes.

Agricultural practices can have both beneficial and detrimental effects on soil fauna (WALLWORK, 1976). Such effects include physical disturbance through ploughing; the reduction in plant diversity with the subsequent effects on litter inputs to the soil and the application of pesticides (COOK *et al.*, 1979; PERFECT *et al.*, 1981). Conversely some groups of soil fauna benefit from improved drainage, irrigation, fertilizer application (RAW, 1967; EDWARDS & LOFTY, 1969) and the maintenance of diverse border habitats such as hedgerows (POLLARD, 1968).

Maize cultivation in the current study significantly reduced the abundance, biomass and diversity of soil macrofauna; only Coleopteran larvae maintained biomass levels possibly due to habitat extension through ploughing and continued availability of food. Although not recorded, the more open habitat of the maize field may encourage termites, especially Macroterminae and *Microtermes* species that have an extensive foraging range and highly seasonal patterns of resource use (WOOD *et al.*, 1977; WOOD & JOHNSON, 1978). Pest species may also benefit from a reduction in predators. Abundances of spiders and adult beetles were low and only 8.3% of monolith samples from the maize field contained ants. Ants were present in all the samples from the mixed woodlot, 83.3% of samples beneath *E. grandis*, 55% of miombo samples and 50% of fallow samples.

Some groups of soil fauna may retard nutrient release by locking up nutrients in persistent faecal material. A subsequent slow release of nutrients may be beneficial to crop production and may buffer against rapid nutrient losses through leaching. Mobile groups such as millipedes may also effect a net transfer of nutrients from edge habitats to the arable fields through the production of faecal pellets. The maintenance of small islands of vegetation with a mixture of indigenous trees between the arable fields may have benefits to soil fertility in addition to the production of fuel wood and fodder. Highest overall population densities and biomass were recorded in the stand of disturbed miombo adjacent to the maize field. This habitat may well act as a refuge and reservoir, particularly for the more mobile species, and aid in the recolonisation of adjacent areas.

The planting of alien trees in the tropics both for building timber and fuel wood has caused much controversy, especially the cultivation of *Eucalyptus* species. The population densities and biomass of the soil macrofauna beneath *Eucalyptus grandis* in the present study were similar to those for the natural woodland. Diplopods were not present in samples but members of the mesofauna, such as Collembola, were abundant.

A hierarchical classification of the habitats based on a soil macrofauna comparison using SØRENSEN'S quotient of similarity (see SOUTHWOOD, 1978) is shown in fig. 4. This analysis suggests a close association between the open canopy miombo habitats and between the mixed woodlot and eucalyptus sites. The last two pairs together with the fallow habitat form a natural

grouping which is distinct from the open miombo habitats. The macrofauna from the maize field shows least similarity with any other site. Clearly the effects of arable cultivation on the soil fauna are greater than other management practices and alter species composition as well as abundance.

5. Acknowledgements

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Synopsis: Original scientific paper

DANGERFIELD, J. M., Abundance, biomass and diversity of soil macrofauna in savanna woodland and associated managed habitats. *Pedobiologia* **34**, 141–150.

Soil macrofauna were sampled from natural savanna woodland (miombo) and four managed habitat types: a maize field, fallow, disturbed miombo and beneath mature *Eucalyptus grandis*. Millipedes and beetle larvae had the largest biomass and were most abundant within the natural woodland. Canopy structure significantly influenced overall population density and biomass of soil fauna with litter dwelling groups most affected by spatial heterogeneity.

Abundance and biomass beneath *Eucalyptus grandis* were comparable with estimates for the natural woodland. Diversity was highest under a small stand of disturbed miombo woodland. Maize cultivation significantly reduced the populations of all groups with beetle larvae the only abundant taxa.

Habitat heterogeneity on a small scale can affect the abundance and composition of the soil fauna community. Retaining some heterogeneity in managed systems would keep areas of favourable habitat and maintain the abundance and diversity of soil fauna.

Key words: Soil macrofauna, biomass, abundance, diversity, tropical savanna, miombo woodland, maize, *Eucalyptus grandis*, fallow, management, habitat heterogeneity.

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